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LIMNOLOGICAL EFFECTS OF FERTILIZING BARE LAKE, ALASKA

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LIMNOLOGICAL EFFECTS OF FERTILIZING BARE LAKE, ALASKA

By PHILIP R. NELSON and W. T. EDMONDSON,[1] *Fishery Research Biologists*

Karluk Lake on Kodiak Island is one of the world's most important red salmon systems. In the early years of the fishery (1888–95) the annual catch alone averaged 3 million red salmon. Since then, a continuous decline in the magnitude of the runs has occurred; in fact, during the period 1944–53 the average yearly run (catch plus escapement into the lake) has amounted to about 1,030,000 fish, just 34 percent of the catch in the early years.

Various explanations of the decline in population may be offered. It might be supposed for instance, that changes at sea may be reducing survival there. Nevertheless, there are good reasons for thinking that the cause of the decline is in the fresh-water phase of the life cycle. A reasonable hypothesis may be stated as follows: with large runs, great quantities of nitrogen, phosphorus, and other important elements were liberated into the lakes when the spawned-out salmon died and decayed. These nutrients were used by phytoplankton, which were fed on by the organisms eaten by young salmon. With intensive fishing, the supply of nutrients to the phytoplankton was greatly reduced, resulting indirectly in lowered production of food for the young fish during their fresh-water phase. The decrease in food supply is supposed to have resulted in increased mortality of salmon either before migrating, or at sea before returning. In the latter case, a decrease in food would probably mean that the migrants going to sea would be smaller, which would result in a higher ocean mortality. Such has been reported by Barnaby (1944), "A greater return, or survival, was found among the older and larger 4-year migrants than among the 3-year migrants." The reasons for developing this hypothesis may now be stated.

The juvenile red salmon spend from a few months to 4 years in the lake before migrating to the sea. During the fresh-water phase of their life history the greatest mortality occurs. Barnaby (1944, p. 294) states, "The mortality of Karluk River red salmon during the fresh-water stage of their life history is usually over 99 percent." While this may be greater than in most areas, it is clear that relatively small changes in mortality may have relatively large effects on survival.

At Karluk Lake the carcasses of spawned-out salmon can furnish a large amount of the phosphorus and nitrogen requirements of the phytoplankton. For example, during 4 years measurements were made of the phosphate at the mouths of tributary streams in the period when the salmon were decomposing in the streams, and on the same streams the phosphate content was determined above the salmon spawning areas, or at the stream outlets prior to the entrance of the fish. Results from this work show almost a fourfold increase (from 0.008 milligram/liter to 0.029 mgm./l.) in phosphate in the stream water during the spawning period of 2 to 3 months. This is a partial figure as it has been found that about one-third of the fish decompose in the stream water while the rest are either removed by animals and birds or washed into the lake before decomposing. Furthermore, it is estimated that 25 percent of the fish in the escapement, the group escaping the fishery and passing into the lake, spawn in the lake and decompose there.

An analysis of the mineral content of canned red salmon (*Oncorhynchus nerka* Walbaum), by Nilson and Coulson (1939), shows phosphorus to comprise 0.3364 percent of the wet weight. Shostrom, Clough, and Clark (1924) found that bone free samples of Karluk River red salmon ran 21.6 percent protein material (3.5 percent nitrogen).

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On the basis of these figures, the decomposition in Karluk Lake of a million spawned red salmon of approximately 4 pounds (1.8 kg.) average weight, approximately 6.7 tons (6,100 kg.) of phosphorus and 70 tons (63,500 kg.) of nitrogen would be liberated. To duplicate this amount in commercial fertilizers would require 37 tons (33,400 kg.) of phosphate at a cost of about $3,000, and nearly 420 tons (381,000 kg.) of sodium nitrate at a cost of nearly $25,000.

Although the size of escapements entering Karluk Lake in the early years is unknown, it may be assumed on the basis of the catch at that time, that prior to fishing, annual runs exceeded 3 million red salmon. In recent years, escapements of 700,000 fish annually account for less than one-quarter of the nutrients formerly supplied.

If this hypothesis states the true explanation for the decline of the salmon population, it can be tested by fertilizing a lake to bring the rate of supply of nutrients to the phytoplankton up to the level probably attained in prefishing years. It should be emphasized that it is not necessary to consider the economics of the conversion of fertilizer into fish flesh. Most growing is done at sea. What is required is merely to fertilize to such an extent that survival is increased significantly.

Although the Karluk fishery is the chief one with which we are concerned, Karluk Lake is so large (total area approximately 14½ square miles) that it appeared desirable to experiment on a small lake where the costs would not be excessive and the results could be accurately assessed. This work should give some indication of the feasibility of fertilizing elsewhere in large lakes.

In 1949, aerial and ground surveys were conducted to find a suitable small lake. Bare Lake, on the southwestern end of Kodiak Island about 15 miles from Karluk Lake, most nearly fulfilled the requirements. From 1950 to 1954 Bare Lake was treated on 7 different occasions with commercial nitrate and phosphate fertilizers.

Primarily, this investigation was designed to determine whether the addition of nutrients would increase the survival of the lake-resident red salmon prior to migration. Although there is evidence of an increase in the size of seaward migrants since fertilization, insufficient data make an analysis inconclusive at this time; a report on this aspect of the work will be made at a later date. The purpose of the present paper is to describe the immediate effects of fertilization on the plankton organisms which are important in the food chain leading to the fish. The bottom organisms, although important, are not treated in this paper.

We thank the men of the United Fishermen of Alaska at Kodiak for their interest and financial help in the work at Bare Iake. We are grateful to the following men for their work in enumerating and identifying plankton: Albert C. Jones, Jr., Robert J. Simon, Melvin R. Greenwood, and Carl E. Abegglen. Field workers who contributed materially in the collection of the data are Carl E. Abegglen, Robert C. Davison, Charles J. Hunter, Carl R. Schroeder, Alfred J. Schroeder, Ralph L. Swan, Robert T. Heg, and Paul H. Hatch. Dr. Phil E. Church of the University of Washington Department of Meteorology, supplied data used in calibrating the light meter. We are grateful to G. W. Whetstone and staff of the Water Resources Division, Geological Survey, at Palmer, Alaska, for making the analysis in table 3.

DESCRIPTION OF BARE LAKE

Bare Lake lies in latitude 57° 11′ N. and longitude 154° 19′ W. It occupies an oval-shaped basin, rather regular in outline (fig. 1). The main axis of the lake lies in a northwest direction and its maximum length is 1,222 meters (4,010 ft.); the maximum width is 495 meters (1,620 ft). The lake is approximately 49 hectares (120 acres) in area, and has a maximum depth of 7.5 meters, mean depth 4.0 meters. Bare Lake can be reached only by air at present.

The lake lies at an elevation of about 380 feet and is surrounded by mountains which rise to a height of more than 2,000 feet. The outlet, flowing from the north end of the lake, is a small stream with a mean discharge of about 6 cubic feet a second (170 l./sec.), which flows into Red River at a point 5 miles distant from the outlet. The lake is fed by one small inlet stream and several small springs.

Species of fish present, in decreasing order of abundance, are the threespine stickleback (*Gasterosteus aculeatus microcephalus* Girard), red salmon juveniles (*Oncorhynchus nerka* Walbaum), dolly varden trout (*Salvelinus malma*

Walbaum), coho salmon juveniles (*Oncorhynchus kisutch* Walbaum), bullhead (*Cottus aleuticus* Gilbert), steelhead trout (*Salmo gairdnerii gairdnerii* Richardson), and king salmon juveniles (*Oncorhynchus tschawytscha* Walbaum). Aquatic vegetation is rather sparse in the lake; water moss, *Fontinalis*, quill wort, *Isoëtes*, and water buttercup, *Ranunculus*, comprise the dominant forms.

METHODS AND EQUIPMENT

During the summers at Bare Lake, analyses of the water were made at the station designated in figure 1. A frame raft was anchored each year at the station to mark the location and from which to suspend bottles for photosynthesis determinations. Water samples were collected with a 3-liter Kemmerer water bottle. Each sample day, water was taken from the surface and from 3- and 6-meter depths.

Dissolved oxygen measurements were made by the Winkler method (American Public Health Association 1946) after tests for the presence of interfering substances proved to be negative.

Measurements of the rate of photosynthesis were made at the surface and at 3- and 6-meter depths. The method, which is becoming a common limnological procedure, was originally described by Gaarder and Gran (1927). These measurements were made by filling pairs of clear glass bottles of 250-ml. capacity with water from each depth. One bottle from each pair was covered with several layers of black cloth and the pairs of bottles were suspended from the raft at the depths from which the water in each was taken. The dissolved oxygen at each depth was measured. After four days the bottles were retrieved and the oxygen content in the light and dark bottles determined. The increase of oxygen in the light bottle (net photosynthesis) is a measure of the oxygen produced by photosynthesis less the amount consumed in respiration, which is measured by the decrease of oxygen in the dark bottle. The total amount produced for the period of exposure (gross photosynthesis) is found by adding the increase of oxygen in the light bottle to the decrease in the dark bottle, or more simply by subtracting the concentration in the dark bottle from that in the light bottle. The measurements are converted to rates by dividing by the time of exposure and are expressed in milligrams per liter of oxygen per day. To permit comparison between our figures and data from other lakes, the volumetric rates at three depths were averaged, each being weighted according to the amount of water at the depth represented, and the averages were converted to a unit area basis by determining the volume of water under 1 square centimeter of lake surface to the mean depth of the lake (4.0 meters).

Certain limitations of the method should be borne in mind. The rate of decrease of oxygen in the dark bottles is a measure of the respiration of the entire biota including the algae. The rate of increase of oxygen in the light bottle therefore is not a true measure of the net photosynthesis of the phytoplankton since there is non-algal as well as algal respiration in the light bottle. However, the rate of increase in the light bottle can be regarded as the net photosynthesis of the entire biota, and is a measure of the momentary balance between the producers and the consumers. Thus when the heterotrophic population becomes too large, oxygen may decrease in the light bottle even with adequate illumination, although it will decrease in the dark bottle faster. The difference is still a measure of algal photosynthesis.

Unfortunately, the rapid multiplication of bacteria in bottled water low in nutrients increases the respiration over that of free water (ZoBell and Anderson, 1936), and the net photosynthesis is underestimated. An assumption of the method is that respiration of all members of the population will be the same in the dark and in the light, as appears to be true for photosynthetic organisms (Brown 1953). While this assumption is not likely to be fully met by other organisms, the differences are probably small enough so that the method is still capable of giving meaningful measurements. Because of the absorption of a small amount of light by the glass of the bottles the rate of photosynthesis may be expected to be slightly underestimated under conditions in which light is at less than optimum intensity. As will be seen, this condition can have affected the present work slightly, since light was not consistently limiting.

Recently Steemann-Nielsen (1952, 1954) has expressed considerable distrust of the bottle technique for waters in which the rate of production was low, although Riley (1953) pointed out objections to the earlier paper. Steemann-Nielsen

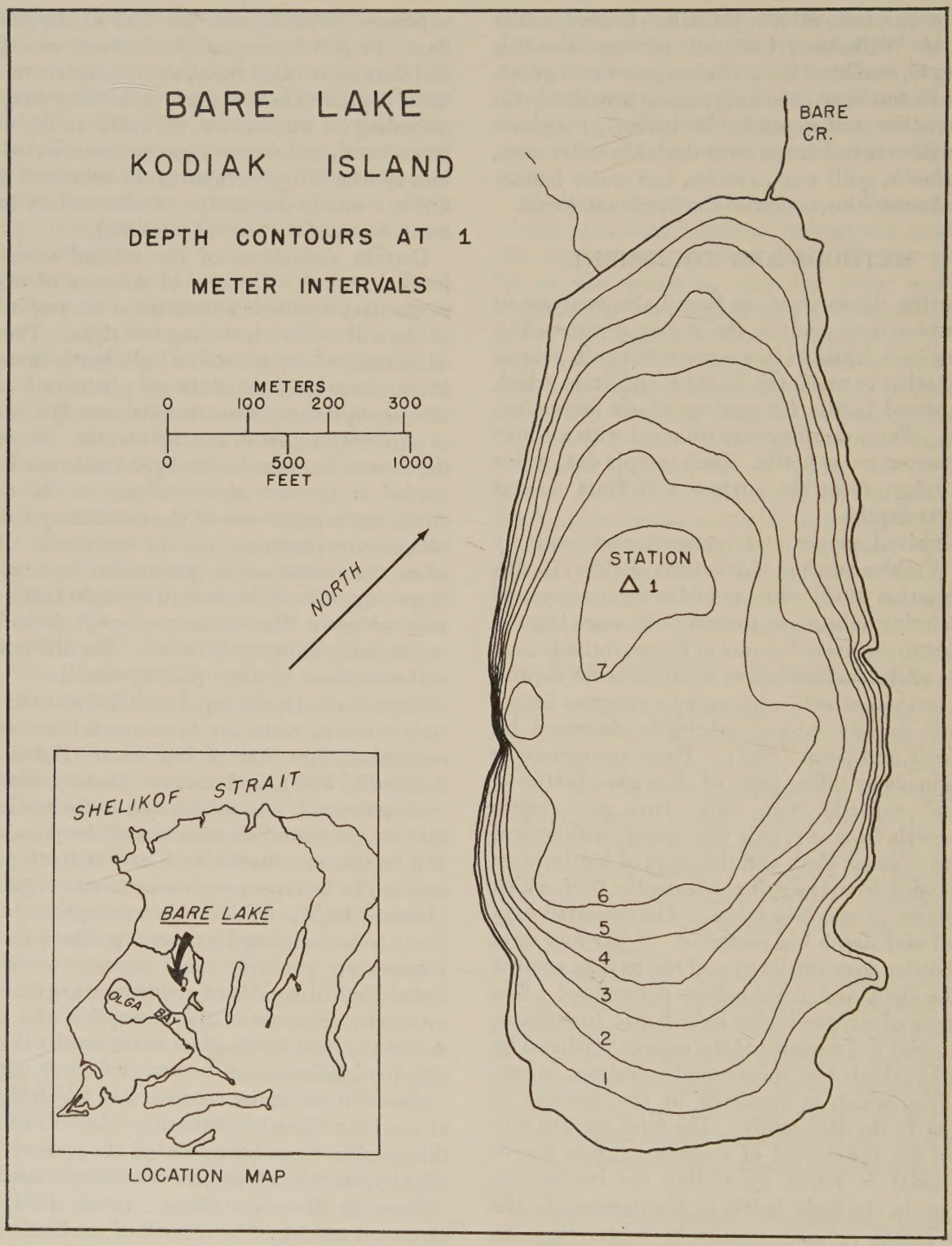


FIGURE 1.—Bare Lake, Kodiak Island, Alaska.

maintained that light has an inhibitory effect on bacteria in the light-bottle. At the moment of writing, a proper evaluation of the method has not been made. It should now be tested with bacteria-free cultures of algae, and cultures to which known quantities of bacteria have been added. In any case, Steemann-Nielsen agreed that useful results can be obtained when production is high. In the present work, greatest emphasis is placed on comparisons between rates before and after fertilization, not so much the absolute rates themselves.

Measurements of the pH were made by the use of a model 607A Hellige comparator.

Temperatures were taken with a Kahl reversing thermometer calibrated in tenths of a degree centigrade.

Free carbon dioxide and alkalinity measurements were both made by the titration methods (American Public Health Association 1946). To minimize the error of loss of CO_2 in the free carbon dioxide test, the method of stirring as described by Ellis and others (1948) was followed.

Soluble phosphorus measurements were made by the method described by Ellis and others (1948); however, one-half of the amount of ammonium molybdate was used (Wattenberg 1937). Measurements of the concentration were made by a 6-volt battery-operated Cenco photelometer which had been calibrated with solutions of known phosphate content. A 5-centimeter cell of 50-milliter capacity and a red filter were used. All determinations on the photelometer were made approximately 6 minutes after the addition of reagents, as the blue color fades with time. Concentrations expressed as mgm./l. of phosphate phosphorus are accurate for small concentrations to within 0.002 mgm./l.

Total phosphorus was determined with perchloric acid digestion, the excess acid being neutralized, and the resulting phosphate determined as described above (Robinson 1941).

Nitrate was determined by a modification of the method of Zwicker and Robinson (1944). Since chloride ions are required to develop the red color, 2 ml. of a 7.8 percent solution of NaCl was added to 4 ml. of lake water and thoroughly mixed before adding 2 ml. of strychnidine. Samples were read in the above described photelometer and the nitrate concentration determined from a plotted curve derived from a similar treatment of standards. For these determinations 1 cm. cells of 10 ml. capacity and a green filter were used. Results expressed in mgm./l. of nitrate nitrogen are accurate for small concentrations to within 0.01 mgm./l. Total nitrogen was determined by a semi-micro Kjeldahl method.

Water-transparency measurements were taken with a Secchi disc.

Intensity of incident light was measured by means of a photographic exposure meter which received reflected light from a white painted surface. The meter was placed within a cylindrical holder 30 cm. above the painted surface and received light from a circular surface having an area of 254.5 sq. cm. Readings were taken three times daily at 9 a. m., 12 noon, and 3 p. m. and are expressed in units of cal./cm.^{2}/min. The instrument, calibrated by comparison with an Eppley pyrheliometer under a variety of meteorological conditions at the University of Washington, proved to have a nearly linear response over the range in which it was used. A table was prepared to convert the reading to the Eppley equivalent as cal./cm.^{2}/min. of total radiation, and for converting the average to daily income of total radiation. In using the data, averages of measurements from four days were calculated to give the mean intensity during the periods which photosynthesis was measured. It is assumed that variations in the spectral composition of daylight are averaged out and that the average composition is constant enough that the limited spectral sensitivity of the exposure meter does not prevent adequate estimate of radiation.

Phytoplankton samples were taken at the surface and at 3- and 6-meter depths at station 1. A sample was placed in a tall cylindrical vessel and formalin added to bring the concentration of formaldehyde to 1 or 3 percent. Four days were allowed for the suspended material to settle. After that time the upper four-fifths of the liquid was drawn off and the residue placed in a vial. Subsequently, the reduced sample was centrifuged at 6,700 r. p. m. for 10 minutes in large tubes with a small calibrated projection at the bottom, permitting the volume of the packed plankton to be measured directly. This is a rather rough index of population size as the degree of packing is dependent somewhat on the character of the organisms.

In addition to the measurement provided by the packed volume, counts of cells were made using a standard method (Lackey 1938).

Net plankton was sampled by pouring measured quantities of water through a No. 20 net and by means of a Clarke-Bumpus sampler. It had been intended to use only the Clarke-Bumpus plankton sampler for zooplankton, and to employ a No. 20 net in order to catch small organisms. All the 1950 samples and those of 1951 through July 23 were taken with the No. 20 net. This fine-meshed net has been used successfully elsewhere (Edmondson 1955), but the dense phytoplankton population clogged the net in Bare Lake, and the watermeter did not work properly. The method was changed, and the rest of the 1951 samples were taken by pouring 80 liters of surface water through a No. 20 net. In 1952 both techniques were employed. A sample of the smaller zooplankton was taken by pouring 3-liter water samples collected at each meter depth from 0 to 6 meters through a No. 20 net. On each sample day two such composite samples were taken at adjacent locations in the lake giving two samples of 21 liters each. The Clarke-Bumpus apparatus was used with a No. 10 net in order to get a proper sample of the larger copepods. In use, the sampler was lowered close to the lake bottom while the boat was in motion and then raised slowly so that all depths were sampled. One revolution of the propeller represented 5.1 liters of water. The samples were counted in aliquots which were either about $\frac{1}{5}$ or in some cases $\frac{1}{25}$ of the whole volume.

When used under conditions in which the net clogs, the water measuring mechanism of the Clarke-Bumpus sampler does not operate properly in that the propellor turns more slowly than it should, and the quantity of water filtered is underestimated. At low rates of flow, the propeller may stop altogether. The critical level at which stoppage occurs, seems to vary among different instruments, possibly having to do with the balance of the propellor.

The effect of this on the results obtained with the sampler used in Bare Lake was studied by towing the net at different speeds and comparing the computed population density with that obtained from the samples in which measured quantities of water were poured through a net. It was found with our instrument that even at low rates of flow, fairly consistent results were obtained. In one series of 7 samples, the coefficient of variation for one of the rotifers was only 25 percent when the rate of turning of the meter varied from as low as 3 to 15 turns per minute, both values well below the range of linearity for most instruments. Ordinarily, it is considered desirable to have a rate of 30 to 40 turns per minute. (C. S. Yentsch, personal communication.) It was found that at the low rates, the results obtained with the sampler overestimated the population density of rotifers and nauplii, but the results were consistent enough to permit us to adjust the 1950 and 1951 data to give a rough measure of the population. The copepodid stages of the copepods seem able to evade the sampler when the rate of flow is slow, and a separate adjustment was made for them. Only samples were used which were well within the range of volume and rate studied, the others were discarded. The samples taken with a No. 10 net present no problems of adjustment. The early samples obtained with the No. 20 net varied from 42 to 339 liters in volume. The 1952 samples taken with the No. 10 net varied from 535 to 1,219 liters. The tows were made at an approximate speed of 2.2 miles (3.6 kilometers) per hour and were ordinarily of 5 minutes duration.

EXPERIMENTAL PROGNOSIS OF PROBABLE EFFECT OF FERTILIZER

Four trips were made to Bare Lake during July 30 to September 23, 1949. An examination of the water was made on the first trip to the lake on July 30. On that date the Secchi disc was visible to a depth of 5 meters. The water temperature was 13.6° C. at all depths, and the water was nearly saturated with oxygen at the surface and bottom. Further analyses showed 4.0 mgm./l. of SiO_2 to be present but no soluble phosphorus was detected. Subsequent trips into the lake were devoted to an examination of the fish fauna; however, it was observed that no visible change in the water transparency took place during the season.

Circumstances prevented extensive work at Bare Lake during 1949. In a preliminary experiment, 18 one-gallon jugs of surface water from Bare Lake were flown to Karluk Lake on August 10. The water was strained through bolting silk to

emove the large zooplankton. One group of jugs as held as a control and to the others were added arying amounts of a solution of KH_2PO_4 and $NaNO_3$ to realize definite concentrations (table 1).

TABLE 1.—*Results of 1949 Bare Lake jug experiment, showing initial concentration of phosphate phosphorus and nitrate nitrogen in each group, production of oxygen and phytoplankton for periods after fertilization and cost of fertilizer on an acre foot basis*

Group	Phosphorus mgm./l.	Nitrogen mgm./l.	Gross O_2 produced mgm./l./day Aug. 10–17.	Phytoplankton cells/ml. (mean for period)		Cost of fertilizer per acre-foot.[1]
				Aug. 11–19	Aug. 21–27	
ug A----	0.000	0.000	0.18	59	149	----------
ug B----	.025	.250	.21	140	----------	$0.16
ug C----	.050	.250	.29	287	1,924	.18
ug D----	.050	.500	.31	391	2,936	.32

[1] 1 acre foot=43,560 cu. ft. or 1,234 cu. meters.

After the addition of the fertilizer, the water as thoroughly mixed, the oxygen content measred, and the light and dark bottles were set out or measuring rates of photosynthesis in the roups. Unfortunately, several of the jugs were ost in a storm, so lack of water prevented photosynthesis determinations after August 17 and hytoplankton counts in group B jugs after ugust 19. In table 1 the gross rate of photosynthesis and the mean phytoplankton population re shown for each series of jugs during periods ollowing fertilization. Also, the cost of the ferilizers per acre foot is given. Of the groups tested it appears that the greatest increase in phytoplankton per dollar resulted from the concentrations used in group C jugs.

FERTILIZATION OF BARE LAKE

One of the initial problems in fertilizing lakes is the determination of the amount and proportion of nutrient elements to introduce. In the carcasses of red salmon the ratio of nitrogen to phosphorus is 10.4 to 1 by weight, but the ratio in algae tends to be considerably lower (Ketchum and Redfield, 1949). The ratio in the fertilizations used was relatively low, about 5 parts of nitrogen to 1 of phosphorus. This ratio is within the range required by algae, and at the same time is relatively economical since nitrogen fertilizers are expensive. The amount of fertilizer to be added was based on the concentration used in jug C of the prognostic experiment. Knowing the volume of the lake, one could add fertilizer annually to increase the concentration of phosphate phosphorus and nitrate nitrogen by approximately 0.05 mgm./l. and 0.25 mgm./l., respectively. This amount is in excess of the concentration which might be obtained from the carcasses of red salmon in a year of a large escapement. However, it appeared advisable to use a larger amount as the success of the experiment depended upon getting a large population of plankton.

The first fertilization at Bare Lake took place on July 12, 1950, when 2,500 pounds of 19 percent super phosphate and 6,500 pounds of sodium nitrate were added to the lake. This amount of fertilizer was calculated to increase the nitrate concentration 0.244 mgm./l. and the phosphate concentration 0.047 mgm./l.

In 1951, the lake was fertilized on July 12 with the same amount of fertilizer as used the previous year. On September 14, 600 pounds of nitrate and 650 pounds of phosphate were divided into approximately equal lots. One lot was placed on a west side beach of the lake, the other lot on an east-side beach, to leach into the water during the fall and following spring.

In 1952, the lake was fertilized with approximately the same amount of nitrate and phosphate as used in the former July applications. However, half the amount was introduced on June 11 and the rest on July 16. Correspondingly, in 1953 very similar applications were made on June 10 and July 15. Table 2 shows when the various fertilizations were made and the expected concentration of nitrates and phosphates which should be realized in the water by the amount added. Also the lapse in time is given before the nutrients were reduced to prefertilization levels.

Two days after each fertilization a series of water samples was taken and the concentration of nitrate and phosphate measured. The mean values for each series indicated that the nitrate had dissolved and the concentration approximated the expected values. Concerning phosphate, less than 20 percent of the amount added could be measured in solution after fertilizations with 19 percent superphosphate in 1950 and 1951 and 47 percent phosphate in 1952. In 1951, a few measurements were made of total nitrogen and phosphorus. Maximum concentrations found were

0.423 and 0.060 mgm./l. of N and P, respectively. The ammonium monohydrogen orthophosphate, $(NH_4)_2HPO_4$, used in 1953, although expensive, is more soluble, and approximately one-half of the amount added was accounted for in solution.

TABLE 2.—*Fertilizations of Bare Lake during 1950–53*

Fertilizer	Date applied	Pounds	Concentration expected mgm./l.		Approximate lapse in days before disappearance [1]
			Nitrogen	Phosphorus	
Sodium nitrate	July 13, 1950	6,500	0.244		17
Super phosphate, 19 percent	do	2,500		0.047	12
Sodium nitrate	July 12, 1951	6,500	0.244		13
Super phosphate, 19 percent	do	2,600		0.049	5
Sodium nitrate	Sept. 14, 1951	600	0.023		
Super phosphate, 19 percent	do	650		0.012	
Sodium nitrate	June 11, 1952	3,300	0.124		9
Super phosphate, 46 percent	do	540		0.025	9
Sodium nitrate	July 16, 1952	3,300	0.124		10
Super phosphate, 46 percent	do	540		0.025	11
Sodium nitrate	June 10, 1953	2,700	[2] 0.125		9
Ammonium orthophosphate	do	500		0.027	5
Do	July 14, 1953	500		0.027	6
Sodium nitrate	July 15, 1953	2,700	[2] 0.125		9

[1] This refers to the interval of time in days following fertilization when the amount of nitrogen or phosphorus added had decreased to the prefertilization level.

[2] The expected concentration includes nitrogen derived from both sodium nitrate and from ammonia in the 500 pounds of ammonium monohydrogen orthophosphate $(NH_4)_2HPO_4$.

The equipment and method used in the application consisted of a 6-man life raft decked over with 2″ x 12″ x 10′ planks on which the fertilizer was hauled. This was towed by a motor-propelled skiff in a zig-zag course over designated sections in the lake. Two men with brooms on the raft swept the mix into the water. Usually the mix was spread in the littoral zone; however, on two occasions it was distributed over the entire lake. Subsequent tests of the nitrate and phosphorus in the water showed no significant difference in the concentrations from the two methods of application.

RESULTS

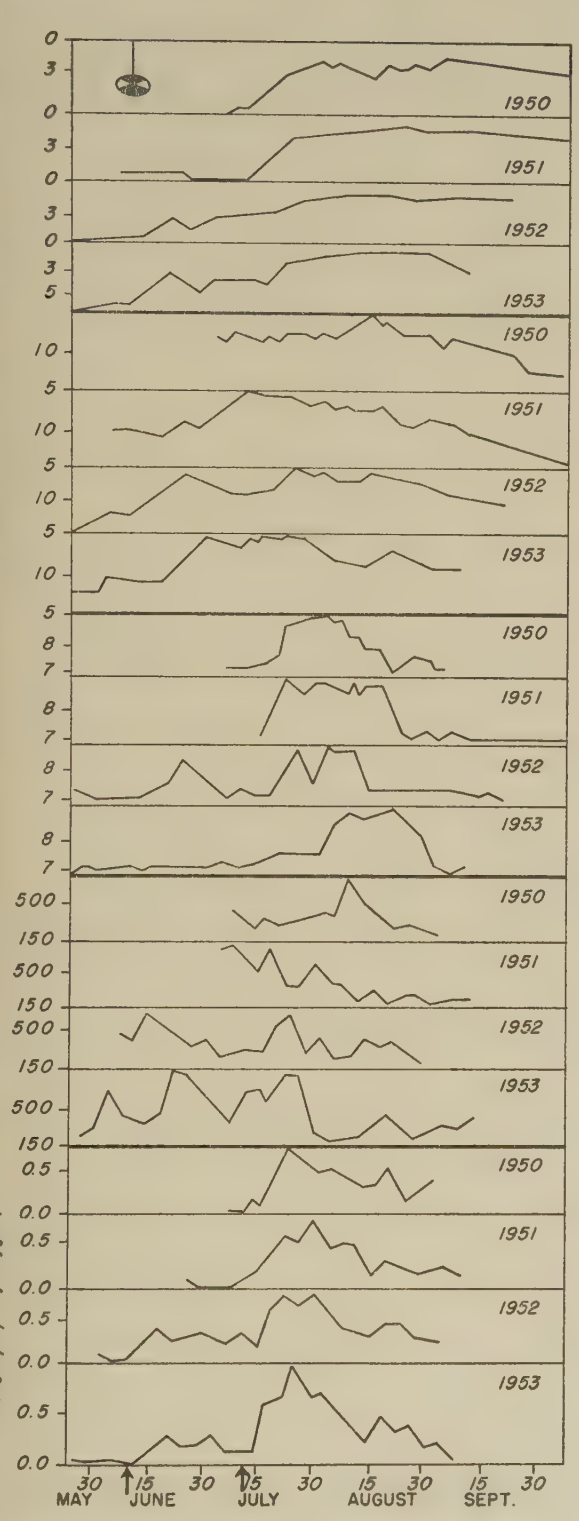
CHEMICAL CONSEQUENCES OF FERTILIZATION

Each year before and after fertilization chemical analyses were made of the lake water. No nitrate or phosphate was detectable prior to fertilization in the four years using the methods as outlined previously. The amount of these elements introduced at fertilization disappeared from the water rapidly. Although some of the material must have been lost to the bottom muds and some utilized by the rather sparse-rooted aquatic plants and moss, the amount taken-up by the phytoplankton created noteworthy changes in the chemistry of the lake.

Before the first fertilization each year the secchi disc reading ranged from 5.5 to 7.0 meters. Following the initial fertilizations the disc reading decreased at the average rate of 1 meter every 3 days for 9 days. About a month later in 1950 and 1951 the readings decreased another meter, whereas in 1952 and 1953 large decreases did not occur until after the second fertilization (fig. 2). Such a pattern in the latter years might be expected as the initial fertilizations were half as large as those of 1950 and 1951. Disc readings were lowest a month after the second fertilizations in 1952 and 1953. In all years the readings had increased by the end of September. Little variation in transparency during the periods of study can be attributed to runoff or meteorological conditions. It should be re-emphasized that such a striking decrease in transparency did not take place in 1949 when the lake was not fertilized.

Free carbon dioxide was present at all depths in the lake each year before fertilization in a concentration of from 0.5 to 2.0 mgm./l. As carbon dioxide was removed from the water by photosynthesis, the increased rate following fertilization reduced the amount of carbon dioxide in solution. From approximately the latter part of July to the latter part of August each year it was absent from the water. Removal of carbon dioxide by photosynthesis reduced the acidity of the water as indicated by the rise in pH values from 7.0 before fertilization to a maximum of 8.8 to 9.3 following fertilization (fig. 2).

Mineral analyses of Bare Lake surface waters were made during the years 1951–53 (table 3). The results show the lake is of the bicarbonate type. Included in the table is a comparison of the concentrations of the major constituents at Bare Lake with the normal concentration occurring in bicarbonate-type lakes having the same specific conductance (Rhode 1949). Bare Lake varies from the normal by having more chloride and sodium and less calcium and bicarbonate. The water is very soft and rather low in dissolved solids. Silica is rather abundant; however, the



amount present in the water has decreased during 1951–53. Following the July fertilizations of 1951 and 1952 large decreases occurred in the silica concentration which probably were caused by blooms of diatoms.

The oxygen concentration remained high at all depths during the seasons of experimentation. As the lake is shallow and often mixed by frequent winds, no stratification of consequence occurred. Measurements of the oxygen production or the rate of photosynthesis before and after fertilization will be considered in the following sections.

RATES OF PHOTOSYNTHESIS

Fertilization of the lake was followed by an immediate increase in photosynthesis, as measured in bottles. Later measurements successively increased for a time, then declined somewhat, appearing to fluctuate around a more or less steady level which was about the same for the 4 years (fig. 3). The second fertilizations in 1952 and 1953 occurred after this condition had been reached, and were followed by large increases in rate. In 1952, the maximum following the second fertilization was insignificantly higher than that which followed the single fertilization in 1951, but was distinctly higher than that of 1950. The highest rate yet observed in Bare Lake occurred after the second fertilization in 1953.

The magnitude of the increase is given numerically in table 4 where the average values are presented for 10-day periods before and after fertilization. The ratio of photosynthesis in the period immediately after the first fertilization to that just before is seen to vary from a minimum of 2.5 in 1953 to a maximum of 7 in 1950. The maximum 10-day rate after the second fertilization varied from 7 to 12 times the prefertilization period.

FIGURE 2.—Graphs of the secchi disc readings, surface water temperatures and pH, light, and gross photosynthesis for the years 1950 through 1953. Arrows denote approximate dates Bare Lake was fertilized (June application in 1952 and 1953, July application in all years).

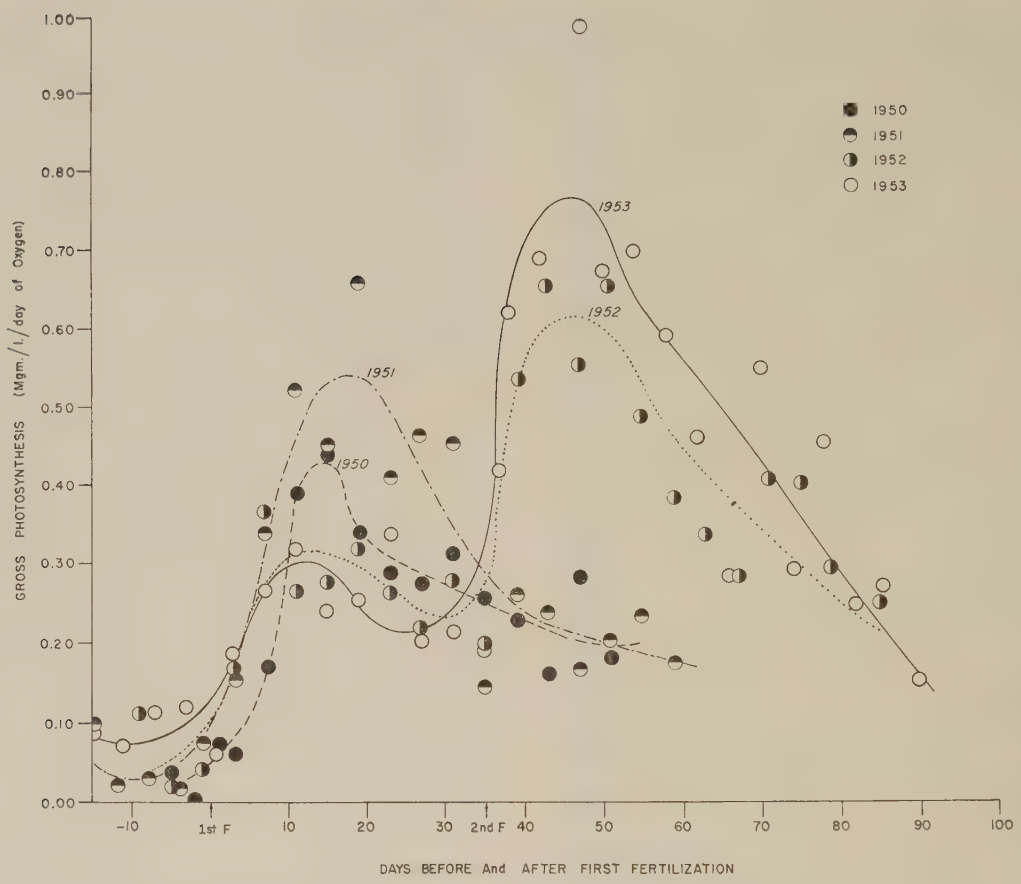


FIGURE 3.—Mean gross photosynthesis of Bare Lake as mgm././day of oxygen. Circular symbols represent mean value during 4-day exposure periods. Curves smoothed by eye show the trends.

TABLE 3.—*Mineral analyses of surface water samples collected at Station 1, Bare Lake, during 1951, 1952, and 1953*

Item	1951					1952						1953						Mean	Normal
	June 9	June 22	July 10	July 15	Aug. 10	May 27	June 16	July 15	July 18	Aug. 19	Sept. 29	May 22	June 14	July 13	July 18	Aug. 24	Oct. 1		
Silica	5.9	6.5	6.0	4.6	7.0	3.7	5.1	5.5	3.4	4.3	4.1	4.2	3.3	3.0	3.0	2.6	2.3	4.4	-----
Iron	0.01	0.01	0.01	0.01	0.03	0.01	0.01	0.03	0.01	0.03	0.02	0.02	0.02	0.02	0.02	0.05	0.03	0.02	-----
Calcium	3.6	3.7	4.2	4.7	3.8	4.8	4.7	4.4	5.6	4.0	4.1	3.4	3.6	3.9	3.7	4.0	3.8	4.1	6.8
Magnesium	1.5	2.0	1.7	1.5	1.8	1.6	1.6	2.1	2.2	1.7	1.7	1.1	1.3	1.6	1.1	1.4	1.1	1.6	1.
Sodium Potassium	5.6	3.4	4.4	3.0	5.6	5.1	5.0	6.0	4.3	7.2	5.9	5.1 0.2	5.1 0.0	5.1 0.1	5.6 0.2	5.0 0.4	5.5 0.4	5.2 0.2	1. 0.
Carbonate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-----
Bicarbonate	16	14	14	13	12	16	16	22	17	20	18	14	16	18	18	17	16	16.3	24.
Sulfate	3.3	3.0	4.0	3.3	4.4	4.4	3.3	3.5	5.8	5.0	4.1	3.7	3.7	2.3	3.7	2.2	2.2	3.6	4.
Chloride	7.5	7.0	8.2	7.2	10.0	8.5	8.8	7.5	8.8	7.5	7.5	8.0	9.2	9.0	8.5	9.2	8.9	8.3	1.
Fluoride	0.1	0.1	0.0	0.0	0.2	0.0	0.1	0.1	0.0	0.1	0.1	0.0	0.1	0.1	0.0	0.1	0.1	0.1	-----
Dissolved solids	35	33	35	31	39	36	37	40	39	40	37	39	41	40	45	46	43	38.6	-----
Total hardness as $CaCO_3$	15	17	18	18	17	19	18	20	23	17	17	13	14	16	14	16	14	16.8	-----
Specific conductance (micromhos at 25° C.)	56.1	53.7	52.4	55.7	59.4	57.7	59.0	61.6	61.4	61.2	60.5	54.9	56.6	57.1	57.8	60.1	58.7	57.9	-----
Ignition loss	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	9	11	10	13	14	13	12	-----

[1] Values in this column are the standard composition of major constituents found in bicarbonate type lakes having a specific conductance of 52 micromho at 20° C. (from table 2, p. 384, Rhode 1949). The specific conductance of 52 micromhos at 20° C. is equal to 58 micromhos at 25° C.

TABLE 4.—*Mean rate of gross photosynthesis during 10-day periods before and after fertilization*

[Upper part: Rates are given as mgm. oxygen per liter per day. Lower part: Rates are given as cal./cm.²/day to permit comparison with the input of solar energy in the same units]

Period	1950	1951	1952		1953	
			First	Second	First	Second
−17– −10		0.03			0.08	
−10–0	[1] 0.02	.04	0.05		.10	
0–10	.14	.28	.25	0.50	.25	0.68
10–20	.39	.52	.28	.59	.27	.74
20–30	.29	.45	.26	.38	.25	.48
30–40	.25	.26	[2] .37	.36	.20	.41
40–50	.22	.20		.31		.33
50–59		.19				.21
Cal./cm.²/day [3]						
−17– −10		0.04			0.11	
−10–0	0.03	.06	0.07		.14	
0–10	.20	.40	.36	0.71	.36	0.97
10–20	.55	.74	.40	.84	.38	1.05
20–30	.41	.64	.37	.54	.36	.68
30–40	.37	.36	.53	.51	.28	.58
40–50	.31	.28		.44		.47
50–59		.27				.30

[1] Period 6 to 0.
[2] Period 30 to 35.
[3] To convert mgm. oxygen/l/day to cal./cm.²/day, multiply by 1.42. This is a composite factor; 1 mgm. oxygen is equivalent to 3.51 cal. The volume under 1 cm.² at mean depth of the lake is 0.405 liters. $3.51 \times 0.405 = 1.42$.

The results show that fertilization was followed by a large and prolonged increase in photosynthesis, and a second fertilization was followed by a swift rise in rate. It may be assumed that the most efficient way of using fertilizer would be to add it in several small doses rather than all at once, since, when several small doses are used, the first dose will develop a large phytoplankton population which can then absorb much of the second dose before it settles out or becomes adsorbed onto the bottom.

In the second fertilization in 1953, phosphate was added alone, followed by nitrate the second day. The nitrate had an additional effect in stimulating photosynthesis, but the magnitude of the effect is hard to evaluate exactly since there were differences in the mean light intensity to which the two sets of bottles were exposed.

The rate at which photosynthesis increased (acceleration) varied somewhat from year to year, but varied only between about 0.026 and 0.044 mgm./l./day/day. These values are approximations of the average rate of increase to the maximum, read from the graphs. The most rapid acceleration in photosynthesis was in 1952 and least in 1953, with 1950 and 1951 intermediate and about equal. The differences are probably a result of the combined effects of differences in light and initial population, but there seems to be no possibility of evaluating the effects separately here. There is no evident correlation with the temperature at time of fertilization.

During the course of each year, large changes occurred in the rate of photosynthesis (fig. 2); to some extent they can be attributed to changes in light, temperature, and population. The shading effect of the greatly increased phytoplankton bloom was probably important in regulating the photosynthesis in the lower water. Before the changes in time can be fully appreciated, a comparison must be made of the photosynthesis at different depths.

VERTICAL VARIATIONS IN PHOTOSYNTHESIS

The vertical pattern of rate of photosynthesis differed considerably from time to time during each year. Most often the maximum rate was at the surface and the minimum at 6 meters, although the distribution was usually not closely exponential. Various degrees of departure from this pattern existed; sometimes the surface and 3-meter rates were nearly alike with the bottom rate distinctly lower, and rarely were the three approximately the same. At other times, the surface rate was distinctly lower than that at 3 meters, and 2 classes of this condition could be recognized; in one the bottom rate was lower than that at 3 meters so that there was a definite maximum in photosynthesis at mid-depth. In the other, the maximum rate was at the bottom, the minimum at the surface.

It was necessary first to examine the distribution of plankton to see whether the differences in photosynthesis can be attributed to this factor. Since the lake was never even weakly stratified for long periods, it would not be expected that the phytoplankton would exhibit strong stratification. Two kinds of evidence are presently available; cell counts (1951 and 1952), and rate of respiration (all years). While both of these measures were nearly uniform in many of the series, there were some fairly large relative differences in vertical distribution. In these, the differences were larger than could be attributed to variation resulting from random sampling from a normal population. Nevertheless, none of the periods of strongly reduced surface photosynthesis coincided with an unusually low plankton content of surface water

Therefore the low surface rates cannot be attributed to low population.

A further examination of the observations was made by cataloging the various patterns of vertical distribution of photosynthesis according to the relative degree of inhibition, and plotting against light intensity, taken as average daily income during the period of each measurement. There was a great scatter in the tabulation, but all 7 examples which had the maximum rate at surface and considerably larger than that at 3 meters occurred with weak light, below 200 cal./cm.^{2}/day of total illumination. The distributions which had surface photosynthesis about equal to or less than that at 3 meters tended to occur at higher intensities. When the data were selected so that only cases were considered in which there was considerable uniformity in the vertical distribution of respiration, the pattern was very much more distinct. Of the 26 selected dates, only 4 showed surface inhibition at relatively low light intensities, and these were all from 1953 at times when the lake was rather transparent.

The observations can easily be understood on the basis of existing data on the relationship between light intensity and rate of photosynthesis by planktonic algae (Manning, Juday, and Wolf, 1938), and the penetration of light into lakes (Birge and Juday, 1929). Since light saturation occurs at an intensity that is only a fraction of full sunlight, and the intensity of full sunlight is distinctly inhibitory, at least when carbon dioxide is present in low concentrations, it may be expected that on bright days photosynthesis will proceed at maximal rate only at some depth below the surface. Surface inhibition is well known from the work of a number of limnologists; the demonstrations by Schomer and Juday (1935) and Curtis and Juday (1937) were based on 3-hour runs in lake water, using uniform suspensions of algae which were kept in unialgal, though not bacteria-free cultures. Since the population in their work was the same at all depths, the lower rate at the surface must have been a physiological phenomenon. Surface inhibition has been demonstrated in longer exposures that include a night (Jenkin 1930 and 1937). Manning and Juday (1941) have presented calculations of photosynthetic rates at different depths in a rather transparent lake at various times of day. During most of the day the surface rate was less than at 1 meter, and at noon, the surface rate was 26 percent of the maximum, which was at 5 meters.

On this basis, it is not surprising that Riley (1940) and Anderson (1954) found very low correlations between light and photosynthesis of natural populations in surface waters, and obtained higher correlations only when considering the entire depth of the lake. Similar calculations for Bare Lake show that during most of a bright day, the maximum rate will probably occur at depths between 0 and 3 meters.

To verify these calculations two special runs were made in 1954, measuring photosynthesis at 1 and 2 meters in addition to the usual depths 0, 3, and 6 meters. The mean rate of photosynthesis for the two runs at each depth, taking the maximum as 100 percent, was as follows, starting at the surface: 89, 100, 87, 69, and 45 percent. The average light intensity was 382 cal./cm.^{2}/day of total radiation, and the results are in good agreement with what would be expected from the works cited in the discussion above.

It is evident that on bright days, our measurements of photosynthesis will somewhat underestimate the actual average rate of photosynthesis in the lake, since the maximum values occur between 0 and 3 meters. The actual amount of underestimation depends upon the actual intensity and the transparency of the lake, but will rarely be more than about 5 percent.

These considerations have led to a much more detailed examination of the vertical distribution of photosynthesis in lakes, but an account of the results would be out of place in the present paper. (See Edmondson 1956.)

VARIATIONS OF PHOTOSYNTHESIS IN TIME

It may be expected that variations in the rate of photosynthesis will be caused principally by changes in the population, in light intensity, in temperature and in nutrition, all of which were measured. Most attention will be given to light.

With respect to the factors causing variations in photosynthesis rates, it is worth mentioning a study by W. T. Edmondson of fertilized phytoplankton populations at the Woods Hole Oceanographic Institution (Edmondson 1955b). In this experiment, nutrients were added to sea

water in large shaded concrete tanks and daily measurements made of photosynthesis, solar radiation, chlorophyll, phytoplankton population, and phosphate. It was shown that almost half of the variation in photosynthesis during the period could be attributed to variations in chlorophyll and solar radiation. Temperature varied little during the period. Interestingly, although there were great changes in the taxonomic composition of the population, there seemed to be no concurrent change in the relationship of photosynthesis with light and chlorophyll; the quantity of chlorophyll was evidently more important in determining the rate of photosynthesis than was the taxonomic position of the cells containing the chlorophyll.

The quantity of chlorophyll showed a very low correlation with cell count, a better though still low relation with total volume of phytoplankton material. While it is unfortunate that conditions did not permit measurements of chlorophyll at Bare Lake, an analysis of the photosynthesis-chlorophyll relationship was not the main objective of the work.

Examination of the graphs of photosynthesis and light in Bare Lake (fig. 2) shows that while some of the major changes were simultaneous, the highest rates of photosynthesis did not coincide with the brightest days; this phenomenon is in agreement with the previous discussion of vertical variations in rate of photosynthesis.

EFFECT OF FERTILIZATION ON THE EFFICIENCY OF THE LAKE

As an initial step in analyzing the response of photosynthesis to fertilization, and to permit comparison with other lakes, a calculation was made of the gross efficiency of the lake, that is, the ratio of the energy used in gross photosynthesis to that available at the surface of the lake. The efficiencies are expressed as percentages of solar radiation and can be considered units of photosynthesis accomplished per calorie of energy. To conform with previous practice by other authors, the solar energy input is taken as the total radiation. As pointed out by Comita and Edmondson (1953) who made a summary of available data on lake efficiencies, it would be somewhat more realistic to use visible light as the basis of the calculation. On such a basis, the published efficiencies would be at least doubled since visible light is about one-half the total radiation (Kimball 1928).

The effectiveness of the fertilizer in raising the efficiency of the lake is strikingly demonstrated when the average efficiency for the entire period following fertilization is compared with that before (table 5), being larger by more than an order of magnitude in 1951 and 1952. It should be noted that the figures in the upper part of table 5 refer to an arithmetic average of the plotted individual efficiencies for each determination. This value will be different from the ratio of the average photosynthesis to average light during the longer periods; the latter is also given in the lower half of table 5, since it is comparable to most published values.

It is unfortunate that we are not able to present measurements of the efficiency for an entire summer without fertilization, for it must be expected that in prefertilization years Bare Lake probably developed a larger population than that found at the beginning of the seasons under discussion. Nevertheless observations of 1949 and pre-fertilization values in July of 1950 and 1951 compared to values in early July of 1952 and 1953 after fertilization, are sufficient to make it almost certain that the rates observed after fertilization are very much larger than anything likely to be found in the unfertilized lake.

TABLE 5.—*Gross efficiency before and after fertilization calculated in two ways*

[In percent]

Duration of time	1950	1951	1952	1953
Mean of individual efficiencies for each 4-day determination:				
Before fertilization	0.018	0.009	0.010	0.036
Entire period after first fertilization	.096	.149	.149	.169
Between the two fertilizations			.098	.059
After second fertilization			.192	.235
Ratio of mean photosynthesis to mean light during entire period:				
Before fertilization	.016	.008	.009	.033
Entire period after first fertilization	.092	.135	.128	.115
Between the two fertilizations			.085	.054
After second fertilization			.165	.186

The fact that light was usually at or above saturation level for photosynthesis is clearly demonstrated in figure 4 where efficiency is plotted against the mean daily light income during the 4-day period of the measurement. The highest efficiencies are at the lowest intensities. It happens that many of the low intensities and high

rates came at such a time after fertilization that the efficiency would be expected to be high. To give some idea of the effect, points representing times of high population (total cell count) are marked for 1951. The marked points have a distinct trend in that they occur in the upper half of the field of points as might be anticipated.

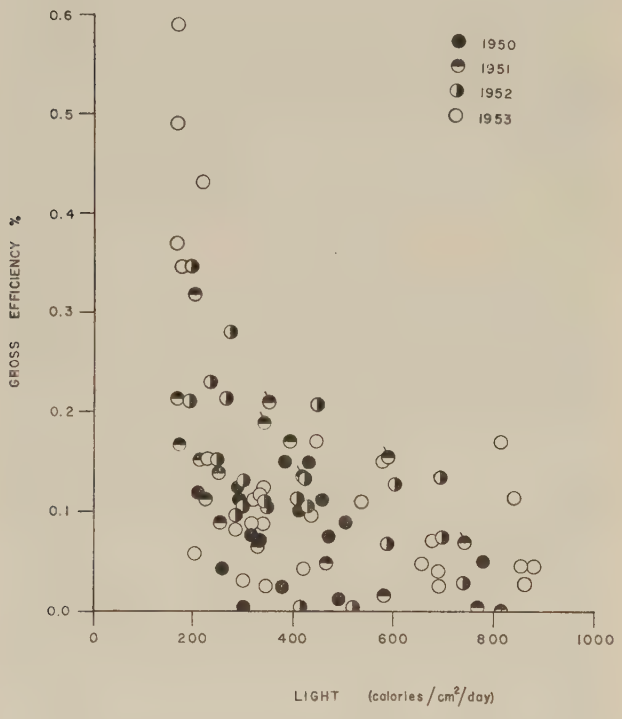


FIGURE 4.—Correlation diagram showing the relationship between total light and the gross efficiency in percentage. Circles represent the mean light and efficiency during 4-day exposure periods. Ticks extending from 1951 symbols denote times of high phytoplankton population (total cell count).

PHYTOPLANKTON

Data on phytoplankton population are available for 1951 and 1952. As would be expected from the large and immediate effect on photosynthesis, fertilization was followed by a rapid increase in the population of photosynthetic organisms (fig. 5). For purposes of the present paper, the population size is characterized by the total cell count. In addition, a few easily recog-

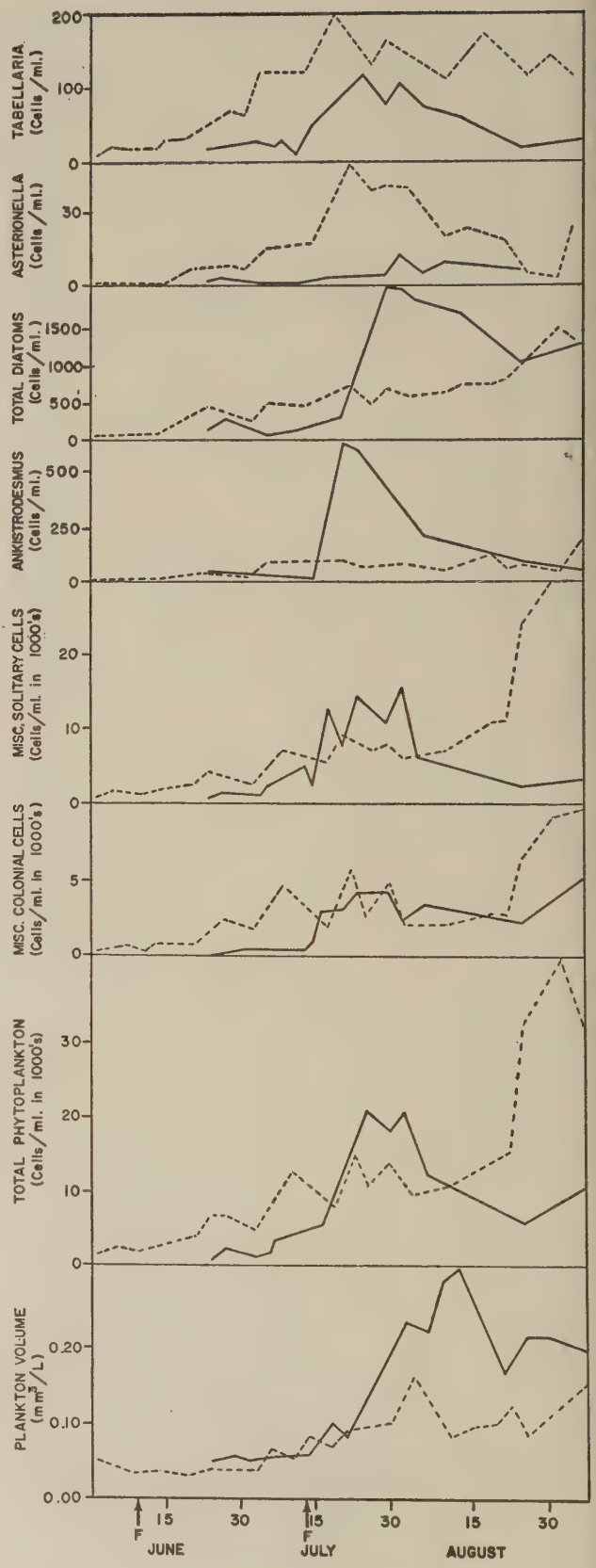


FIGURE 5.—Seasonal abundance of phytoplankton during 1951 (solid line) and 1952 (dotted line). Arrows denote fertilization dates during the two years (July 12, 1951, June 11 and July 16, 1952).

nized genera are listed, and the rest of the population cataloged as miscellaneous solitary cells and miscellaneous colonial cells. When authoritative identifications of our material have been made it will be possible to present a discussion of the specific changes in population composition, and to present data representing the mass of the total population and its components.

As an additional measure of distinct but limited usefulness, we have recorded the packed volume after centrifugation. Unfortunately, this measure varies with the strength of preservative when there are many filamentous algae present; apparently the filaments are stiffer and pack less closely when preserved with 3 percent rather than 1 percent formalin. The packed volume shows about the same trends in total cell count, except the total cell count in 1951 showed a considerable rise to a maximum density more than 10 times that of the prefertilization period, after which it declined. In 1952 the maximum population was somewhat lower but after the second fertilization eventually achieved a size about 20 times prefertilization level. The rate of rise was very different in the 2 years. While there were differences in temperature, they are insufficient to explain the difference in rate of rise, particularly in view of the data on photosynthesis. The curve for packed volume followed that for total cell volume rather well at first, but showed striking departures during the latter part of each year, indicating considerable changes in the makeup of the population.

The comportment of different organisms was strikingly different in the 2 years. In 1951, *Tabellaria* decreased after its maximum in the middle of the summer, while in 1952 the population reached a higher level for the rest of the summer. *Asterionella* was a very inconspicuous member of the population in 1951, and while in 1952 it never became abundant, it was in fact several times as abundant as during most of 1951. Conversely, *Ankistrodesmus* which showed a very sharp rise in 1951 maintained low numbers in 1952.

It would be improper to generalize from these data about the effect of fertilization in encouraging or discouraging particular forms. Carlin has shown (1943) that in unfertilized waters great changes in the relative dominance of different species of phytoplankton and zooplankton can occur from year to year during a 6-year period.

In terms of cell numbers, the average for the two years shows little difference except that produced by a great increase of several forms at the end of the season in 1952. Cell volume appeared to be somewhat higher in 1951 than in 1952. While the difference is in the same direction as that observed for photosynthesis (table 4), it seems somewhat out of proportion. A reduction in standing crop of algae could result from increased grazing activities by the zooplankton.

ZOOPLANKTON

In this study, the zooplankton organisms must be considered because of their importance as consumers and transformers of phytoplankton. The zooplankton organisms at Bare Lake are to a small extent of direct use as food of the very young fish, and some of them may be of indirect use to larger fish if they are eaten by larger benthic organisms such as Tentipedid larvae. The zooplankton organisms may be of significance in another way, as competitors with some species of the bottom fauna for phytoplankton food. Each adult zooplankter at the end of its life represents at least several times its own bulk in consumed food. As the zooplankton make up a very small portion of the food of the fish, these animals represent a diversion from the end product which is regarded as important. Even if the bottom fauna contains species capable of eating small zooplankton, there is still a loss of efficiency with each additional interposed trophic level.

While the return of salmon will be the empirical test of the hypothesis on which this project is based, any satisfactory explanation of the results must be based on consideration of the distribution of matter through the entire biota. Because of the nature of the food and reproduction of the zooplankton, a delay may be expected in the manifestation of the results of fertilization. Not only must the phytoplankton first increase to a degree that will increase the effective reproductive rate of the animals, but time for a number of generations must pass before a greatly enlarged population develops. Moreover, if there are predatory animals present whose feeding efforts match the increased rate of food production, little elevation in population-size may be found. Animals with a long generation time may show effects only after more than a year. With these considerations in

mind, some aspects of the zooplankton populations will be examined, but others will be more profitably considered after measurements from several more years have accumulated. An interesting discussion of production in an aquatic community has been given in detail by Harvey (1950).

Rotatoria

The rotifer populations consisted of a variety of species. Those forming the largest populations are equipped to feed on very small organisms or fine particles of detritus, namely, *Keratella cochlearis* Gosse; *Kellicottia longispina* (Kellicott), *Conochilus unicornis*[2] Rousselet. Others are predatory, capable of piercing small animals and sucking out the contents as *Ploesoma truncatum* Levander, *Ploesoma hudsoni* Imhof, and *Synchaeta pectinata* Ehrenberg, or swallowing small animals, as *Asplanchna priodonta* Gosse. Of the former group only *Ploesoma truncatum* appeared in relatively large numbers. *Ploesoma hudsoni* was consistently present, but formed less than 1 percent of the entire *Ploesoma* population. It is well known as a voracious rotifer, and may have been the cause of much zooplankton mortality. Other species found in small quanities were *Polyarthra vulgaris* Carlin[3] and *Gastropus stylifer* Imhof.

Two of the important rotifers, *Keratella cochlearis* and *Kellicottia longispina* carry eggs attached to the lorica. The eggs were counted as well as post-embryonic animals in the expectation that a sudden increase in food supply might be indicated by an abrupt increase in the ratio of eggs to female. A sudden increase in the production of eggs would be followed by a period in which many of the females would be immature, and the ratio would decrease even if the rate of egg production by the adults remained the same. The period of embryonic development and immaturity may amount to more than 4 days in some species, although data are not available for the present species under consideration at the temperatures prevailing in Bare Lake.

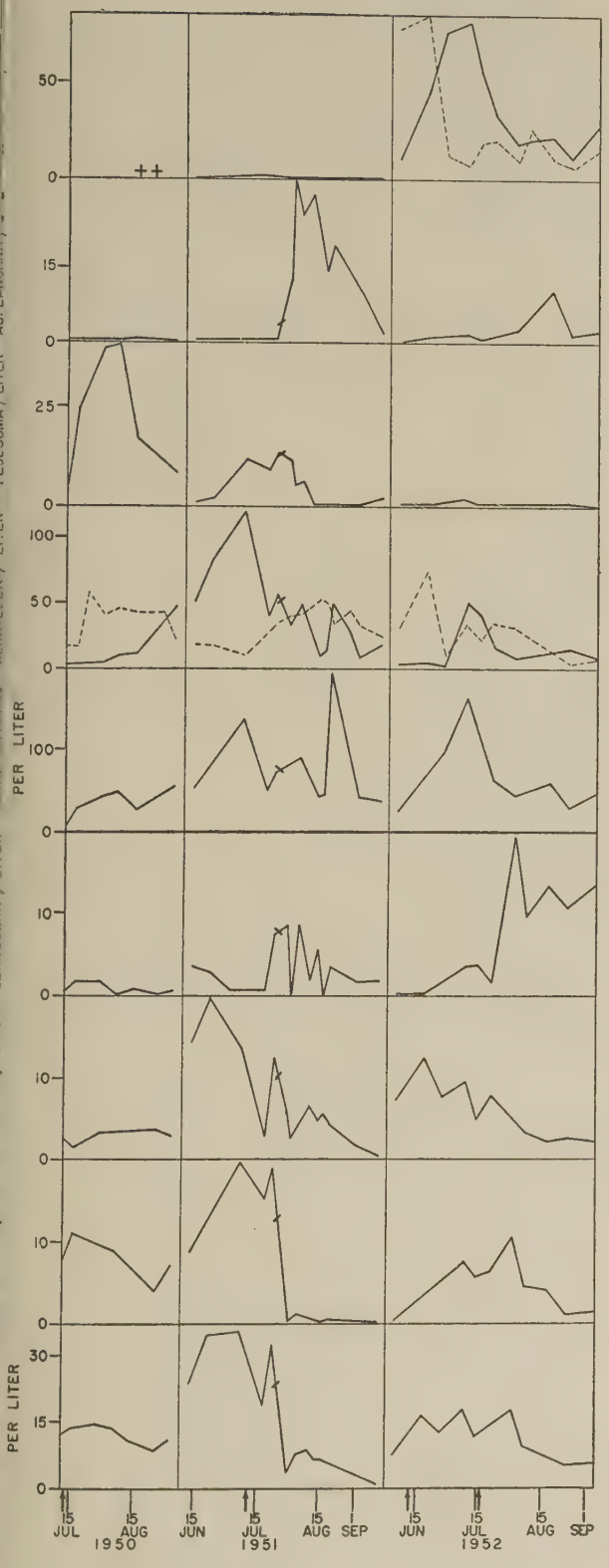
[2] The contracted specimens were named on the basis of one undivided coronal antenna. Since it may be that a number of species with one antenna have been grouped under the name *unicornis*, the identification should be regarded as provisional.

[3] This is the *P. trigla* of many authors. Carlin asserts that it is now impossible to assign the name *trigla*.

The seasonal changes in the more abundant species were considerable (fig. 6). The data plotted have been selected so that intercomparison is possible. All data plotted are based on collections with the No. 20 net, the No. 10 net samples being used only for larger organisms. Unfortunately, it was necessary to change the technique of collection during 1951, and the samples after July 23 refer only to the surface population. The apparent change in population size cannot be entirely attributed to the difference in technique, since as will be shown, the mortality of some species actually increased. In any case, the data of 1950 and 1952 should be comparable, and those of the first part of 1951 with 1950.

The graphs are self-explanatory, but some features deserve comment. *Keratella cochlearis* formed the largest population observed in the 3 years, but in 1952 it was surpassed by *Kellicottia longispina*. Both species might be expected to benefit by an increase of small algae or of bacteria, and can be regarded as competitors. About a week after fertilization in 1950, the egg ratio of *Keratella* had doubled, and remained high until the end of the season when it fell somewhat. In 1951 there was a similar change, but rather slower. In 1952, the greatest value of the ratio ever observed occurred 6 days after fertilization. *Kellicottia* was abundant enough to permit profitable calculation of the ratio only in 1952. The ratio, which was high in the first collection, was even higher in the collection 6 days after fertilization, and fell subsequently, showing fluctuations during the rest of the year.

Ploesoma truncatum is known to kill *Keratella cochlearis*, and in fact two of the collections contained a *Ploesoma* fixed in the act of pumping out the contents of a *Keratella*, having first grasped it by the corona. It is interesting therefore to see some suggestion of reciprocal relationships between the populations of the two species. In 1950, when the population of *Keratella* was small, *Ploesoma* was at its 3-year maximum. After the *Ploesoma* population had fallen drastically in 1950, *Keratella* increased. In the prefertilization period of 1951, the 3-year maximum population of *Keratella* developed and began to fall off in the presence of a smaller *Ploesoma* population. A very large population of *Asplanchna*, known to kill *Keratella*, developed late in July, and *Kera-*



tella fell to a low level. The quantitative details are obscure here because of the necessary change in sampling technique, but qualitatively there seems little doubt about the decline, especially in view of the fact that an unusually large number of empty *Keratella* loricae were observed in the sample of July 29 in company with an increasing number of *Asplanchna*.

The events in 1952 were rather different from those of the previous year in that some of the previously important species were especially scarce; i. e., *Ploesoma* and *Keratella* were represented by small populations. *Kellicottia* on the other hand was consistently present, and achieved its 3-year maximum. The largest *Kellicottia* population in 1952 occurred in the period before *Asplanchna* developed its maximum population.

Copepoda

The only copepod to occur in important numbers was *Epischura nevadensis* Liljeborg, kindly identified by Dr. G. W. Comita. Occasionally a small cyclopoid occurred in the samples. Although mature *Epischura* were found during much of the season, and females were collected bearing spermatophores, egg sacs occurred in only two collections. It appears that the egg sacs drop rapidly to the bottom.

Counts were made of nauplii and copepodids separately. The earliest collection of any year, June 3, 1952, contained nauplii and early copepodid stages only. Adults were not found until the middle of July. The first sample of 1951, June 13, contained no adults, the oldest copepodid collected probably was stage 4, judging by the appearance of the appendages, although a sample collected on June 14 contained a mature male. Mature specimens were present in numbers on

FIGURE 6.—Seasonal abundance of rotifers and crustaceans during 1950, 1951, and 1952. Arrows denote fertilization dates. On July 23, 1951, for the rest of that year the technique of collection was changed. Marks on the 1951 curves denote that date. Only selected rotifer species are shown separately. Time of occurrence of *Kellicottia* in 1950 is shown by plus signs as the numbers are too small to plot. The number of eggs per female is shown by dotted lines as percentage for *Keratella* and *Kellicottia*.

July 7. In 1950, mature specimens were present in all the collections.

In the first two years, the copepodids were most abundant in the first collections, and showed a general decline during the year. A possible explanation would refer to the predaceous rotifers which can attack nauplii and small copepodids. The population was reduced to a very low level at the end of 1951 which may account for the lower initial population in 1952 and the smaller average. Only the year 1952 shows the expected generally reciprocal relationship between abundance of nauplii and copepodids, the copepodids increasing as the nauplii decreased.

The copepods have such a long generation time that it is not to be expected that the quantity will increase immediately after an increase in phytoplankton. While the numbers may be expected to increase over the years, the fact that they do not increase greatly can be understood if they are effectively fed on by predators.

Other crustaceans

No crustaceans other than copepods were quantitatively important in the lake. There were a few Alonella, Chydorus, and other very small Cladocera. It is noteworthy that no Daphnia was ever seen. Some samples contained ostracods, but not in large quantities.

DISCUSSION

As far as we have ascertained, this is the first published account in which measurements of photosynthesis have been used to diagnose the productive condition of a fertilized lake, although the technique has been used in unfertilized lakes (e. g., Riley 1938) and in a fertilized salt-water bay (Edmondson and Edmondson, 1947). In most previous studies, reliance has been placed on changes in standing crop of phytoplankton, zooplankton or benthos, or growth of fish. In some, changes in phytoplankton density have been gauged by changes in secchi disc transparency (Ball and Tanner, 1951, Raymont 1947, Gross and others, 1947, 1950). In other cases, emphasis has been on following the added nutrient elements into the biota in different regions of the lake (Einsele 1941) or small bodies of water confined in tanks (Pratt 1950). Although the addition of radioactive phosphorus cannot be considered a fertilization, it gives useful information about the rates of uptake, exchange and distribution (Hutchinson and Bowen 1947, 1950, Coffin and others, 1949, Hayes and others, 1952).

While the standing crop of food organisms at any moment may be a measure of the availability of food to the predatory population at that moment, it may not be by itself a good measure of the rate of supply of food to the predators. The literature on fertilization of all kinds of waters indicates that ordinarily fertilization will be followed by an increase in the mass of many components of the biota. The work of Gauld (1950) is important in showing that the effect of fertilization on phytoplankton may not be apparent as an increase in the standing crop because of active grazing, which absorbs the increased production. Even when there is an increase in crop, it may not be in proportion to the increase in primary production. It is possible that the same effect may be found at other trophic levels; a copepod that has contributed to the growth of a fish will not be counted in a plankton sample.

The data presented in this paper show that certain limnological effects of fertilizing Bare Lake were immediate, prolonged, and great. Photosynthesis increased immediately, and was soon followed by a large increase in the quantity of phytoplankton. The reproductive activity of the rotifers was likely affected, but our data do not show a general increase in the abundance of zooplankton. Nevertheless, evidence is accumulating that the food supply of the fish has probably been increased. (U. S. Fish and Wildlife Service, unpublished records.) An analysis of the bottom fauna will be of interest when completed.

In conclusion, we should emphasize certain facts about the investigation. The main point of the work was to provide conditions by fertilization which would cause a great increase in the food supply of young red salmon, directly or indirectly. Thus, we were not making a study of fertilization as such, and we did not plan to make recommendations as to proper kinds and amounts of fertilizer. Such work can be more effectively done in more accessible lakes at lower latitudes where laboratory conditions permit elaborate analyses. It was not possible to establish a control in the form of an unfertilized lake, but this lack is not serious

n evaluating the immediate limnological effects, n view of the observations of 1949 and general mnological knowledge of the production of lakes. n the Bare Lake work, the initial quantity of ertilizer was chosen to fit certain requirements, nd was repeated the second year without modi- cation although it was obvious that less fertilizer ould give satisfactory results. Since the second ear, the fertilization program has been varied, he major concern being to obtain large effects. hus, in 4 years we have a variety of additions f fertilizer, but in each case, the primary produc- ion of the lake has been greatly increased, and his is the essential requirement of testing the ypothesis on which we are operating.

The lack of a formal control may be important n connection with the survival and growth of he fish; however, some data of this nature are ollected annually from the large lakes in the area, nd these may offer a valuable comparison. It s planned to continue studies in Bare Lake for any years, alternating periods of fertilization ith periods in which the lake is left unfertilized. his program may be expected to give more satis- factory results than one of short duration in which complete dependence is placed on a control lake.

For a complete understanding of the effects of ertilization, as full a set of measurements as pos- ible must be made. The interpretation of meas- rements of photosynthesis in terms of possible rowth rates requires further critical study, but hotosynthesis seems to be the most direct meas- rement available, and one which permits very apid diagnosis of the degree of effectiveness of a given fertilization. The technique of fertilizing jugs of water variously and observing the photo- synthesis and standing crop for a period of time offers many possibilities for prognosis, and is capable of great development and refinement. A good many of the interpretations of populations depend on specific knowledge of algal physiology, much of which does not yet exist for important planktonic species, although a good beginning has been made (Chu 1943, Ketchum and Redfield 1949, Osterlind 1949, Rodhe 1948, Gerloff and others 1950, Vollenweider 1950, Burlew 1953).

The physiological condition of a population is so important in determining its productivity that it is doubtful that a list of species counts and a few simple chemical determinations will ever be sufficient to characterize a population for the purpose of assessing productivity or predicting the results of fertilization. The response of a population to changed conditions, as added nutrients or reduced grazers, will probably be found to be important information on which to base an assessment of productivity, or on which to base a program of fertilization. The development of improved techniques for such assessment is surely promising with increased knowledge of productivity.

It is possible that even with fertilization the return of salmon to a given lake will not be increased for reasons which have nothing to do with the success of fertilization. The data reported in this paper represent part of the information which will be used to evaluate the effect of fertilization and to interpret the final results of the experiment. If the fish population is successfully increased in Bare Lake but not in Karluk, we can relate the difference to a definite measure of basic productivity. If the return of fish is not increased, at least we will have information which may contribute to an explanation.

A discussion of the results of the fish investigation is not part of the present paper, but it is of interest to comment that each year since fertilization salmon leaving the lake have been distinctly longer and heavier than the year before (unpublished data).

SUMMARY

1. Bare Lake, a 120-acre unstratified lake on Kodiak Island, Alaska, was fertilized in 4 successive years with commercial inorganic phosphorus and nitrogen fertilizers.

2. The quantity of fertilizer was in part decided on the basis of prognostic experiments in which jugs of Bare Lake water were fertilized and the increase of photosynthesis and population measured.

3. The effect of fertilization on the rate of photosynthesis by the existing population in the lake was immediate and large. The rate in the 10-day period after fertilization was increased by a factor of 2.5 to 7 as compared to the 10-day period before fertilization.

4. The rate of photosynthesis progressively increased after fertilization, then fell to a rather

steady level well above the initial value. A second fertilization resulted in a rate greater than the first maximum.

5. Light was supraoptimal, photosynthesis at the surface frequently being about equal to, or less than at 3 meters. The highest efficiencies of utilization of sunlight occurred in periods of relatively low light. Efficiency was increased by fertilization.

6. Following each of the yearly fertilizations the phytoplankton population increased manyfold, the transparency decreased from about 6 to less than 2 meters and the pH increased from 7.0 to a high of 9.0. Phosphate and nitrate fell to an undetectable level in a few days.

7. Some rotifers seemed to show an effect of increased food supply in that egg production was apparently accelerated.

8. The planktonic crustaceans did not show a significant increase in population size from 1950 to 1952, possibly as a combined result of their long life cycle and effective predation.

9. Salmon leaving the lake have been longer and heavier in successive years, suggesting that they are responding to increased food supply.

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